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SHORTER ARTICLES AND DISCUSSION

CAN SELECTION CAUSE GENETIC CHANGE?

It is almost a pleasure to have occasion for controversy with a fellow worker who shows himself so fair-minded and generous an opponent as does Dr. Pearl in the *AMERICAN NATURALIST* for February, 1916. He credits my investigations with greater merits than I have claimed or can claim for them. If they possess any superiority, it is not because they have been either better planned or better executed than Dr. Pearl's, but only because the material used was more favorable. In my experiments with rats I have simply undertaken a less difficult task than that undertaken by Dr. Pearl in relation to the fecundity of fowls. Pearl is right in supposing that I have no desire to convey the impression that his work is valueless. No one has greater admiration than I for the masterly way in which he has analyzed the fundamental problems of genetics and the thorough and systematic way in which he has attempted their solution. I regret only that he has courageously attacked so complex a problem before certain simpler and more elementary ones had been solved. I felicitate myself only on having been content with a less ambitious program.

I am pleased to learn too that we are so closely in agreement as regards the observational facts, that in reality it is only concerning the *interpretation* of results that our views seriously differ.

I am quite ready to grant that we are concerned with the same fundamental question, that of the possible quantitative change in a character under selection, that the methods which we have employed are substantially the same and that these methods are open to similar objections, that *random sampling* occurs in the rat experiments as well as in those with fowls, though it is involved in a further degree in the experiments with fowls because of limitations of age and sex. I am quite willing that Pearl should recall the statement "that phenotypic variation of the character fecundity in fowls, markedly transcends, in extent and degree, genotypic variation," and that he should substitute in its stead the statement that it "*may*" so transcend. I am even

more ready to concede the existence of genotypic variation in this character than Pearl has shown himself to be. And I have been reluctant to accept at its face value Pearl's statement that at the conclusion of his fecundity selection experiments he had *more* good winter layers than at the beginning, but none *better*. For in our selection experiments with rats it is very clear that when high-grade individuals grow common, a few individuals of *higher* grade are sure to put in an appearance. Genotypic variation seems to me to be of such wide occurrence that it is difficult to believe that it is ever wholly absent, that absolutely pure lines really exist. I quite agree with Pearl's conclusion that somatic character is not a sure index of genetic constitution and that it was therefore entirely logical and necessary for him to make progeny tests in order to classify his pullets genetically. To establish the point it is not necessary for him, as he observes, "to be fussily nasty" by citing page after page from my Mendelian writings. I had granted the point years before it was raised.

This brings us again to what Pearl considers "the most serious phase of Castle's attack, namely that in which he denies the validity of my conclusions respecting the inheritance of the character fecundity in fowls." Let it be made very clear at the outset *what* is attacked. Not the idea that fecundity is inherited. I think that I am even more ready than Pearl to admit that fecundity is a quantitatively variable character and that its various quantitative conditions are inherited. This is merely to state in another way that *genotypic* as well as *phenotypic* variations in fecundity occur. If they occur, it is possible to isolate them and thus to produce families characterized by them. The conclusion which I "attack" is this, that the observed variations in fecundity depend upon two and *only two* differential factors, both of which are Mendelian, one sex-linked and the other not sex-linked. Several possibilities are conceivable, which this conclusion does not include, as for example that *more* than two genetic factors are concerned in the variation, that one or other or both of the supposed factors are quantitatively variable and so capable of gradual change under selection. I am not advocating or defending any of these possibilities. I am merely attacking the conclusion outlined substantially as I understand Pearl to hold it. There are really several distinct points in this conclusion, some of which seem to be better grounded than others. If I were asked either to accept or to reject it *as a whole* (and Pearl's pub-

lished data leaves no alternative to this) I should reject it, and this decision would not be influenced by the consideration that Morgan, Doncaster, Johannsen and Plate accept it, because it accords with the conception of the pure-line which they have adopted. Authority does not count in science. Majorities do not decide what is true. If they did, Mendelism would have been false in 1868 and true in 1900. If Morgan and Johannsen should next week decide against the pure line idea, as Jennings has already done, what could the rest of us then do except change our minds too, if we base our scientific judgments on authority? Dr. Pearl, I am sure, would be the last to advocate such an idea.

I grant to Pearl the legitimacy of his method in attacking the problem of the inheritance of fecundity and the necessity of establishing arbitrary categories of winter egg production in which his birds are then classified. But I regret what seems to me to be the needless restriction of his published data to the contents of these categories. Pearl points out that I too have made use of arbitrary categories in dealing with the rat statistics, but I would call attention to this difference in our procedure. My categories, + 1, + 2, etc., are indeed arbitrary, but I have not limited the reader's information to their contents. I have published the data in such form that the reader may, if he chooses, form new categories with different inclusiveness, subdividing each category and then subdividing these again down to the lowest limit of observation which can be made with certainty. Pearl has not made it possible for us thus to deal with his data. We may take it or leave it, but we can not change it. We have no means of knowing how many pullets laid 1-10 eggs in their first winter, how many laid 11-20, or 21-30 eggs. In what particular are these "original records" which Pearl withholds "valuable" except as proof of the conclusions which he sees fit to base on them? If he decides, as announced, that the data are not to become public property until he has finished his own study of them, he is well within his rights, but what is the hurry about forcing the *conclusions* upon a waiting public? Would not the public be justified in deferring its decision as to the validity of those conclusions until data as well as conclusions are available?

Pearl seeks to offset his own sin of omission by charging a like offence upon me, maintaining that the scientific public withholds acceptance from my conclusions concerning the rat selection experiments solely because I have never presented my results "in

such form that any other interpretation of the data could by any chance be tested." If this statement is true, it is because of my inability to devise any other form in which to present the data. I have presented it in such form that the limits adopted for the categories of variation could be shifted at will and I am ready to be shown how its presentation can be further improved and simplified. Pearl suggests that my omission pertains to the individual pedigree of the rats, in which suggestion he echoes a thought of the Hagedoorns on which I have twice commented elsewhere, showing, I think, that the alleged defect does not exist, for the following reasons:

1. It is impossible for a colony of 33,000 rats to be produced from an original stock of less than a dozen animals, with constant breeding together of those which are alike in appearance and pedigree, and with continuous selection of extremes in two opposite directions, without the production of pedigrees which in the course of each selection experiment interlock generation after generation and finally become in large part identical with each other. This has been repeatedly verified in individual cases, but is incapable of a more generalized statement or of demonstration in generalized form. At least I am unable to devise such demonstration.

2. In a specific case described on pp. 20 and 21 (Castle and Phillips) a selection experiment was started with the hooded F_2 offspring of a single selected hooded and a single wild rat and this experiment was carried through the F_8 generation leading to the production of 804 young from rigidly selected, closely inbred descendants of a single pair. We showed (l. c., p. 21) that the progress of selection within this inbred family follows a remarkably close parallel, generation by generation, to the progress of selection in our plus series as a whole. Here there can be no question of a difference in pedigree among the selected animals. This is eliminated as a possible factor in the result. Can Pearl suggest any other possible factors capable of elimination? If so, I should be pleased to give attention to them.

I humbly beg pardon for having made the all too obvious suggestion that environmental conditions, and in particular size of flock, may affect average flock fecundity. And yet I find that Pearl himself elsewhere lays great stress on this point. My chief offense seems to lie in my failure to realize that he had already taken all possible precautions in this matter, and that he consid-

ered himself in a position to vouch for the uniformity of environmental conditions, not only in eight years of experiments which he had personally superintended, but also in nine previous years of experiments of which he had neither control nor information until they were completed and which were made sometimes in 50, sometimes in 100, and sometimes in 150 bird flocks. Are there not here some elements of uncertainty which at least condone the offense even if they do not excuse the question?

I am prepared to accept without question Pearl's statement that date of hatching can not possibly have had anything to do with the rise in average flock production which has occurred between 1908 and 1915, notwithstanding his own previous statements on the subject and the evidence which Phillips has produced that date of hatching of ducks affects their adult size. I am prepared to accept the view that this rise was due wholly to genetic changes, but I do not believe that Pearl or any one else is in a position to say to what agencies the decline previous to 1908 was due.

And now, with Pearl, I turn with pleasure to the general problem of selection and note that our differences are here rather verbal than real. They lie in that philosophic pitfall of *causation*.

Pearl can not conceive that selection may *cause* or *occasion* or *lead to* genetic change, though he can readily see how populations may change under its influence. Thus selection may increase the proportion of high-grade individuals but it can not, on his view, beyond a limited and fixed point, occasion the production of individuals of increased grade. With these views I squarely take issue, and I shall try to show that his view is a purely *a priori* view, while mine is based on both observation and experiment.

Pearl's reasoning throughout rests on the assumption that the potentiality of a germ cell can not change except by a *causeless* method, "mutation"; that no extraneous influences can change it. Experience teaches directly the contrary, indicating that germ-cells brought together in fertilization mutually *influence each other*. Let us consider for a moment Pearl's illustration. He supposes an organism to exist, A_{ss} , which is producing gametes of the uniform value, a_{ss} , and can not understand how such gametes uniting with each other can ever produce individuals of a higher value, say A_{30} . No more can I, if we accept his further

hypothesis that there is to be "no mixing of germ-plasms." But what justification have we for that further hypothesis? Experience furnishes none. On the contrary, I have shown in numerous specific cases that when unlike gametes are brought together in a zygote, they mutually influence each other; they partially blend, so that after their separation they are less different from each other than they were before. The pure-line advocates have adopted the procedure of dismissing such explanations as mystical, an easy way to dispose of troublesome ideas. But the stubborn fact remains to be accounted for that partial blending does occur (1) when polydactyl guinea-pigs are crossed with normals (Castle, 1906), (2) when long-haired guinea-pigs are crossed with short-haired ones (Castle and Forbes, 1906) and, (3) when spotted guinea-pigs or rats are crossed with those not spotted (MacCurdy and Castle, 1907). Davenport has furnished numerous instances of the same thing in poultry; indeed he has shown that "imperfection of dominance" and of segregation are the rule rather than the exception in Mendelian crosses in poultry. To assume that "there is no mixing of germ-plasms" is a contrary-to-fact assumption, whatever it may be in formal logic or scientific methodology.

Let us change slightly Pearl's hypothetical case. Let us suppose, as he does, that a gamete a_{38} has united in fertilization with another a_{38} gamete producing a soma, A_{38} . Now what sort of gametes may we expect such an individual to produce? Pearl says, in effect, nothing but a_{38} gametes, unless a genetic miracle occurs, a mutation, incapable of casual explanation. But we should hesitate to characterize as miraculous anything which occurs with regularity, and experience shows that this is what happens quite commonly, if not regularly, in such cases. The A_{38} individual produces gametes a *majority* of which have the value a_{38} , but a few of which have a higher value, a_{39} , and a few a lower value, a_{37} . For the correlation in value between soma and gamete is not absolute. It is in many cases close, but not invariable, as I think Dr. Pearl would admit. If it be granted for the sake of argument that gametic variation occurs, it is obvious that we have grounds for expecting somatic variation in the following generation. For an a_{39} gamete uniting with another gamete like itself may be expected to produce a zygote of value A_{39} . Pearl maintains that such an event is without "causation," is incapable of prediction and control, that all we can do is to

record its occurrence, a view I by no means share. But, it may be asked, *what control* can we exercise over the event? We can prevent or permit it at will. For observation shows that if we permit the individual to mate only with those of inferior value, we shall get no offspring of the highest grade. Thus $a_{33} + a_{36}$ produces commonly only A_{37} , rarely A_{38} and, we might say, never A_{39} . But if we permit the individual to mate with individuals of *equally* high grade (and this is what selection in a particular direction does) experience shows that a majority of the offspring will be of that same grade, but a *few* will be of higher grade. These few make possible further advances. Thus a_{39} makes possible the subsequent attainment of a_{40} . Whether this relationship involves "causation" or not is a question for the logicians and methodologists, of whom I am not one. As to the *fact* our rat experiments leave no doubt. In the light of such facts it seems to me that a view earlier held among biologists, that variability is one of the fundamental properties of organisms, comes nearer to the truth than this modern notion of the pure, unvarying line. This pure-line concept Pearl rightly characterizes as "one of the most useful working tools in the practical breeding of plants and animals that has ever appeared." Why useful? Because it has caused us to pause and take careful inventory of our facts, and to discard as rubbish many loosely held notions. But Pearl reminds us that not all the pure linist's facts are in one basket with Johannsen's beans, nor even in that other vanished basket with Jennings's paramecia. There are, he reminds us, "all the Svalöf oats and wheats to be reckoned with." True and they are mute witnesses to the cumulative effects of selection. For all agree that these pure lines of oats and wheats are the product of continuous self-fertilization. And what more than self-fertilization renders possible generation after generation the union of gamete with its like, the indispensable condition for progressive variation in a particular direction, as I have tried to show?

Intelligent selection only accelerates this natural process of progressive variation, for it singles out the individual which is producing gametes of unusual value and permits the union of such high grade gametes only with gametes of their own sort, so that step after step in a particular direction becomes possible, where unguided self-fertilization would give only halting and uncertain progress. Can we doubt that it is progressive varia-

tion guided by rational selection in a particular direction that has made possible the doubling in size that most of our domesticated animals have undergone since they were taken from the wild state? And does any one seriously think that a *single* selection from wild stock has produced for us the enormous horses of Flanders, or the little ponies of the Shetland Isles, the enormous sheep of the Scotch highlands, or the huge rabbits of Europe, each a monstrosity in comparison with its most probable wild ancestors, and yet producing blends in crosses with them? This blending shows that the change has been one of slow accomplishment and not the result of sudden discontinuous change.

When we compare the color varieties of domestic animals with those of their wild ancestors, as I have been able personally to do in the case of covies, we are struck by the fact that the domestic varieties are relatively clear and distinct in color, either more intense, more dilute, or of purer color than we can obtain from the wild form by simple recombination of genetic factors. For example it is possible by crosses to obtain from wild covies the retrogressive varieties, black and yellow. But such synthetic blacks lack the full intensity of blackness found in our best strains of black guinea-pigs, and the synthetic yellows are apt to be either pale or muddy in yellowness, lacking the intensity and brilliancy of our best domestic varieties. It is impossible to escape the impression that our improved domestic varieties are not mere factorial recombinations derived from wild species, but that they have been forced up to a higher standard by repeated selection; that the breeder, for example, has first observed variation in intensity of blackness among his blacks (doubtless obtained originally from a retrogressive sport) and that by repeatedly selecting the blackest available individuals he has increased the blackness of the race. Thus it is no accident that the meat and milk and wool producing capacity of our domestic animals far exceeds that of any wild ancestral species. The standard in each case has been raised and it has not been raised by a single lucky accident (the mutation view), but by a series of slow advances each impossible until a previous advance had been made. I am aware indeed that Pearl at one time maintained an opposite view, holding (if I remember correctly) that our best strains of poultry are no better layers than *some* strains of jungle fowl. But I do not believe that this view can be successfully defended. I am certain that such an idea is quite preposterous in

the case of most characters for which our domestic animals are valued and as regards which their *improvement* has been attempted by selection. In such cases there has been a *series* of slight advances, and everything indicates that the *order* of the advances is significant and necessary, that the higher stages can be attained only by passing through the lower ones. If this is so, we need not quibble about "*causation*," but we may assure ourselves that if we wish to attain a distant goal, the first thing to do is to make for intermediate points.

I regard it as a hopeful sign that Pearl can see no reason why genetic changes may not be small in amount in some cases, even though large in others. This I hope is only a first step toward the complete abandonment of that "real, genuine pure-line body of doctrine" which he still holds dear.

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